Studies of Behavioral State in *Aplysia*

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Abstract. This paper reviews a series of studies on the neural organization and the cellular mechanisms underlying behavioral states; in these studies, feeding behavior in *Aplysia* was used as a model system. Feeding in *Aplysia* has similarities to motivated behaviors in other animals and is modulated by a number of interesting state variables, including arousal. Food-induced arousal manifests itself in two categories of feeding behavior: (1) appetitive responses (*e.g.*, head-up feeding posture and directed head turning), which orient the animal to potential goal objects such as food; and (2) consummatory responses (biting, swallowing), which obtain the goal object. The consummatory responses are rhythmic and relatively stereotyped, whereas the appetitive responses are highly variable. Our evidence suggests that one consummatory response, biting, appears to be controlled by command elements in the cerebral-ganglion, such as neuron CBI-2, which are capable of driving the behavior. One component of the appetitive behavior, head lifting, may be controlled (at least in part) by another cerebral neuron, C-PR. C-PR, however, affects numerous systems in the animal, but all the systems affected seem to be involved in the food-induced arousal state of the animal. We postulate that C-PR is, in some ways, analogous to command neurons that evoke behaviors. The C-PR, however, not only evokes a behavior, but also evokes a central motive state which aids in insuring that behavior is efficiently expressed.

Introduction

Mollusks have long been used for studies that are designed to investigate general neurobiological principles rather than the details of a single species. One important advantage of mollusks is the large size of their neurons.

For many years, studies that were difficult or impossible in vertebrates could be approached by investigating the squid giant axon and the large somata of gastropod neurons. In recent years, the use of cell culture, brain slices, and other methodologies has made it possible to do many types of cellular studies on vertebrate neurons that could previously be done only in mollusks. However, it is still very difficult to study the integrative functions of the vertebrate nervous system and to relate cellular processes to behavior. For this reason, the presence of a relatively few neurons in gastropod mollusks has assumed increased importance.

We have been studying the marine mollusk *Aplysia* in order to understand the neural organization and the cellular mechanisms underlying behavioral states. We have concentrated on feeding behavior because our early studies indicated that the feeding responses of these animals are modulated by a number of interesting state variables, including arousal and satiation (Kupfermann *et al.*, 1982; Susswein *et al.*, 1978). This paper is a review of our work. It emphasizes studies of the appetitive aspects of feeding, and is not meant to be a general review of feeding in *Aplysia*.

Feeding Behavior in *Aplysia* has Similarities to Motivated Behaviors in Other Animals

To provide themselves with adequate nutrients, *Aplysia* has many of the same problems faced by most other animals. They must detect and locate appropriate food sources. They must approach the food and orient it to the buccal orifice. They must then bite and swallow the food. Finally, when a sufficient amount has been consumed, they need to stop feeding. These operations must all be carried out in a manner that is efficient in time and energy expenditure. One of the means by which the animals im-
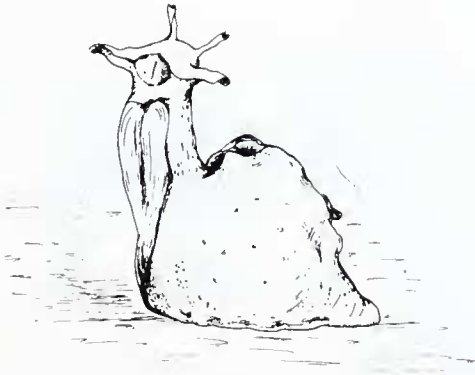
Figure 1. *Aplysia* in the feeding posture. In this position the animal shows directed turning responses to seaweed applied to the head.

Figure 3. Turning angle evoked by repeated seaweed (open circles) or tactile (filled circles) stimuli. The animals (n = 5) were first induced into the feeding posture by means of seaweed. They were then stimulated at a locus 10° from the mouth, either with a purely tactile stimulus, or with seaweed. The stimulus was repeated every 10 s (10 successive stimuli; 3 series each). Final turning angles of the responses are shown as the percent of the final angle of the first response (means ± S.E.M.). Note the marked decline in the magnitude of the turning response evoked by repeated tactile stimulation and the relatively steady response magnitude upon repeated seaweed stimulation. Data from Teyke *et al.* (1990b).

prove the efficiency of their behavior is by regulating it according to particular internal states. These internal states are modulated by external and internal stimuli and by an internal endogenous process associated with a circadian activity rhythm. In higher animals, the constellation of state variables that regulate feeding are termed "hunger," and by analogy, a hunger-like state also appears to regulate feeding in *Aplysia*. As in higher animals, feeding in *Aplysia* is greatly potentiated by pre-exposing the animals to food; *i.e.*, the animal exhibits incentive motivation. When a quiescent *Aplysia* is first stimulated with seaweed, it becomes activated after a relatively long delay (up to a min-
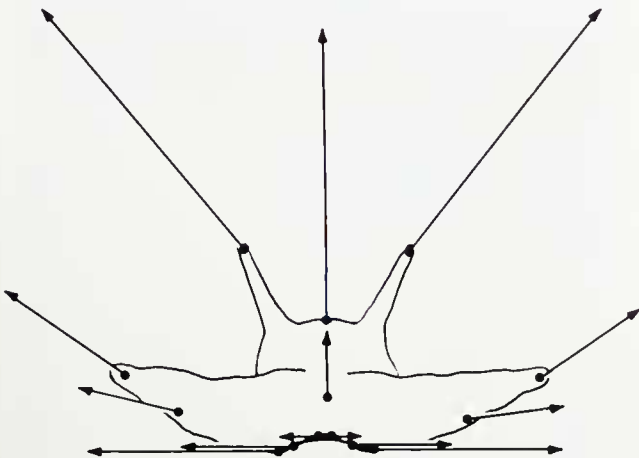

Figure 2. Vectors indicating the magnitude and direction that the head turns in response to tactile stimuli briefly presented (open loop) to different points on the rhinophores and tentacles. The movements turn the head in the direction of the stimulus. In the open loop condition the animal greatly overshoots the stimulus. If, however, the stimulus is maintained in place (closed loop), when the animal begins the response, the movement is represented by the indicated vectors, but as the animal turns, the response progressively decreases in magnitude so that the mouth comes to be accurately centered over the stimulus. Data from Teyke *et al.* (1990b)
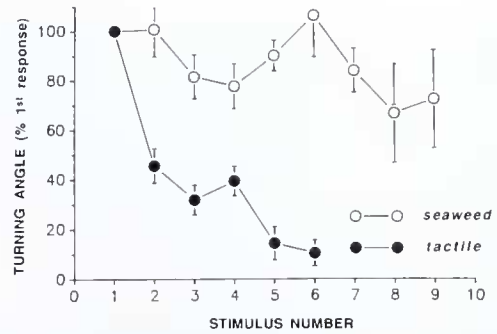
ute). We refer to this activated state as "food-induced arousal."

Food-induced arousal in *Aplysia* manifests itself in at least two stages. First, appetitive behaviors (the orienting phase of motivated behaviors) are affected; second, consummatory responses are modified. Initial contact with food evokes a defensive withdrawal reflex of the head. The fast phase of this reflex appears to be controlled by the cerebral Bn neurons (Teyke *et al.*, 1989), which receive powerful tactile input, and which evoke withdrawal movements of the head and tentacles. After the initial defensive response, the animal ceases to withdraw. The response appears to be habituated, but unlike other forms of habituation in *Aplysia* (Castellucci *et al.*, 1970, see also Fig. 3), the response decrement occurs very rapidly, typically following just a single application of the stimulus. A subsequent brief food stimulus elicits an orienting response, instead of eliciting withdrawal. The animal gets into a characteristic feeding posture in which the posterior part of the foot is attached to the substrate, and the neck, head, and anterior part of the foot are lifted (Fig. 1). In addition, there are signs of "autonomic" arousal, such as an increase in blood pressure and heart rate (Koch *et al.*, 1984). The feeding posture is maintained even when the food is removed, indicating that the appetitive arousal has a "memory" component. From the feeding posture the animal can readily move its head toward a source of food. When the tentacles of the food-aroused animal make physical contact with food (seaweed), the animal moves its head so as to direct its mouth towards the stimulus (Fig. 2). For a brief (open loop) stimulus within the receptive field, the animal greatly overshoots the food, and the amount of overshoot is proportional to the angular
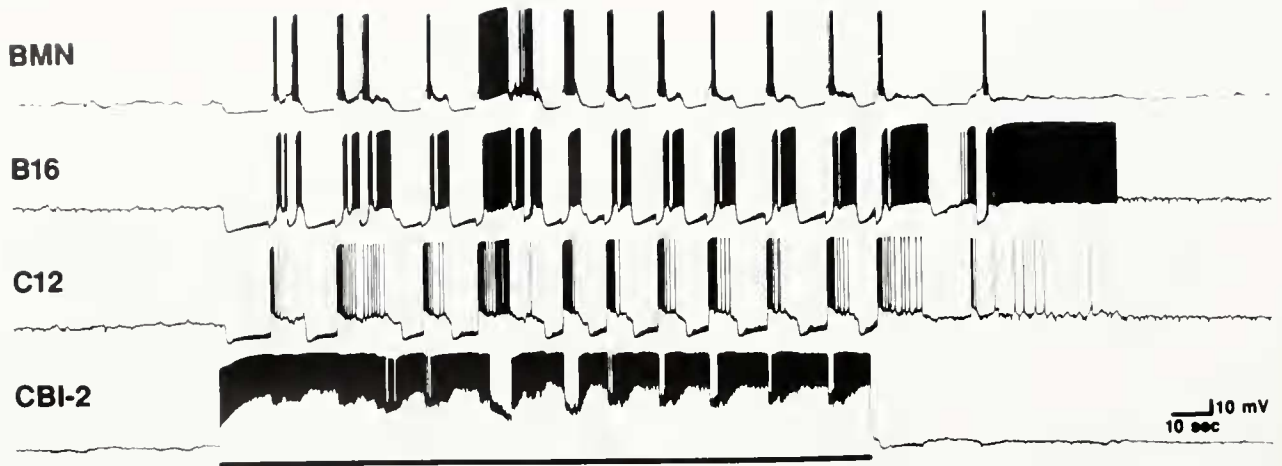
Figure 4. Example of the motor program driven by CBl-2. CBl-2 was fired by a constant depolarizing current (dark horizontal line). The rhythmic program incorporated neurons in the cerebral and buccal ganglia. The buccal program is reflected in the activity of an identified ARC muscle motor neuron, B16. Another buccal motor neuron, BMN, illustrates that the program is present in numerous other buccal neurons. C12 is a cerebral ganglion neuron that controls movements of the lips, and it is one of several cerebral neurons that is recruited by the buccal program that is driven by CBl-2. CBl-2 also shows periodic synaptic input driven by the buccal program. Note that when CBl-2 stops firing, the program briefly persists and then terminates. The data are from Rosen *et al.* (1987, 1988).

distance of the stimulus from the mouth. If, however, the stimulus is maintained in position so that it provides continuous feedback during the movement (closed loop), the food is accurately centered over the mouth (Teyke *et al.*, 1990b). Seaweed provides the animal with two distinct types of stimuli: tactile and chemical. Surprisingly, the stimulus that results in the animal turning toward the food is the tactile component. A purely chemical stimulus, provided by an aqueous extract of seaweed, is not very effective in eliciting turning. On the other hand, if the animal is first aroused with a chemical stimulus, a purely tactile stimulus (provided by a glass rod) very effectively evokes a turning response. If, however, the tactile stimulus is repeated without intermittent chemical stimulation, the turning response habituates until no response at all is evoked (Fig. 3). Thus, the chemical component of the seaweed maintains the arousal level of the animal, while the tactile component directs the response.

When the animal turns toward the stimulus, contact with food to the region immediately around the mouth (perioral zone) initiates consummatory behaviors and a new set of arousal responses. The consummatory arousal is characterized by a progressive build-up of the rate and magnitude of the rhythmic biting response that occurs when food touches the perioral zone (Kupfermann, 1974; Weiss *et al.*, 1982). Whereas the appetitive feeding responses are highly variable, the consummatory biting response is more stereotyped, although it consists of several components (Kupfermann, 1974; Weiss *et al.*, 1986): (1) There is a forward movement (cocking) of the whole buc-

cal mass. The forward position is maintained during the whole meal. (2) The whole buccal mass undergoes forward and backward movements. These movements occur on a background of the maintained forward movement. (3) The radula rotates forward and backward. (4) The radula halves open and close. The latter two movements cause the food to be grasped and deposited into the buccal cavity. The relatively small backward movement, which deposits the food in the buccal cavity during biting behavior, can be distinguished from a larger backward movement (swallowing) that is triggered by the presence of food in the buccal cavity, and which results in the food being moved into the esophagus (Kupfermann, 1974). Biting movements, which are elicited by food contacting the perioral zone, thus consist of a large forward component of the radula, followed by a relatively small backward movement. Swallowing, which is elicited by food in the buccal cavity, consists of a relatively small forward movement and a large backward movement. The swallowing movements are associated with an inhibition of the biting movements; *i.e.*, as long as food is present in the buccal cavity, stimulation of the perioral zone never elicits a large forward movement of the radula.

Biting Responses are Elicited by the Activity of Individual Neurons Located in the Cerebral Ganglion

In a number of species, including gastropod mollusks, stereotyped responses are elicited by the activity of individual cells or small groups of cells (Kupfermann and
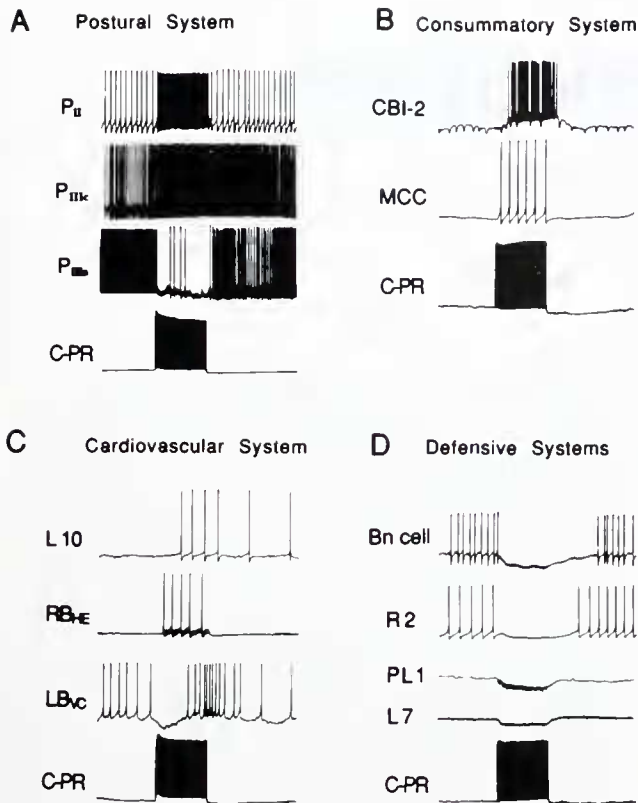
Figure 5. The various effects of firing C-PR on different systems associated with food-induced arousal. For each experiment, C-PR was intracellularly stimulated at 20 Hz for 5 s. For illustrative purposes, multiple follower cells of the C-PR are shown for each part of the figure, but the data for each trace were obtained in separate experiments. (A) Examples of the effects of firing C-PR on different pedal ganglion neurons, that may be part of the postural control system. (B) Effects of C-PR on cerebral ganglion neurons that control consummatory feeding responses (biting command element, CBI-2, and the modulatory neuron, metacerebral cell, MCC). (C) Effects of C-PR on abdominal ganglion neurons that control the cardiovascular system (command element L10, heart exciter RBHE, and vasoconstrictor LBVC. (D) Effects of C-PR on various neurons that participate in defensive responses [head withdrawal neuron, Bn cell (Teyke *et al.*, 1989); gill withdrawal motor neurons, L7; defensive secretion neurons, R2 and PL1]. Calibration: 2 s, 20 mV, except 5 mV for cells R2 and PL1 in part D. Data are from Teyke *et al.* (1990a).

Weiss, 1978; Gillette *et al.*, 1982; McClellan, 1986; Benjamin and Elliott, 1989; McCrohan and Kyriakides, 1989; Delaney and Gelperin, 1990). To determine the critical control elements for the consummatory phase of feeding in *Aplysia*, we back-filled the cerebral-buccal connectives and located a population of cerebral neurons that send their axons to the buccal ganglion. Several of these cells had been previously identified, including the serotonergic metacerebral cells (MCCs) and ICBM mechanosensory cells (Rosen *et al.*, 1989a,b). In addition, two small populations of cells were found in anterior and lateral positions. Firing of one of the cells (cerebral to buccal interneuron two, or CBI-2) within the anterior cluster, produced a robust and reliable rhythmic motor program of the buccal ganglion (Fig. 4) (Rosen *et al.*, 1987). CBI-2 receives chemosensory input from the perioral zone. In addition, when it elicits a buccal motor program it receives rhythmic synaptic input from the buccal ganglion, and thus it fires in phase with the buccal motor program. If, however, the synaptic feedback from the buccal ganglion is blocked by placing the cerebral ganglion in seawater containing cobalt ions, the firing of CBI-2 still evokes rhythmic activity in the buccal ganglion, in the absence of rhythmic activity in CBI-2 (Rosen *et al.*, 1988). For a discussion of recent work on the central pattern generating circuitry intrinsic to the buccal ganglion of *Aplysia*, see Kirk (1989), Nagahama and Takata (1989), and Susswein and Byrne (1988).

Using a semi-intact preparation, we found that the firing of CBI-2 can evoke rhythmic movements of the buccal mass and radula, and the movements are similar to the repetitive biting responses seen in the intact animal. The responses do not resemble swallowing or rejection. The firing of two other cerebral to buccal interneurons also evokes coordinated buccal ganglion activity, but the motor programs are different for each of the CBIs. Thus we hypothesize that the CBIs in *Aplysia*, as in other gastropods (Gillette *et al.*, 1982; Benjamin and Elliott, 1989; McCrohan and Kyriakides, 1989; Delaney and Gelperin, 1990), may constitute a command system, the conjoint activity of which drives consummatory feeding responses.

Activity of an Identified Cerebral Neuron Appears to Elicit Elements of Appetitive Arousal

Although stereotyped consummatory responses are driven by a relatively few command-like elements, it is difficult to imagine how the highly variable responses that constitute appetitive behavior could be similarly driven by a small number of neurons. Nevertheless, we set out to determine whether the nervous system contains neurons that can evoke appetitive feeding behavior. Backfills of the cerebral-pedal connectives revealed a small subset of cerebral ganglion neurons that send their axons to the pedal or pleural ganglia (Teyke *et al.*, 1990a). The firing of these neurons revealed a single (bilateral) cerebral neuron that can influence the activity of numerous neurons in the abdominal, pedal, and cerebral ganglia. We termed this neuron the cerebral to pedal regulator [to avoid confusion with the caudal photoreceptor (CPR) interneuron of crayfish, we abbreviate this neuron C-PR, although previously we did not use the hyphen].

The pedal ganglion in particular contains a large number of neurons that are excited by C-PR (Fig. 5). A smaller number of pedal ganglion neurons are inhibited by C-PR. Each neuron that is affected by C-PR activity receives input following the firing of either the left or right C-PR,
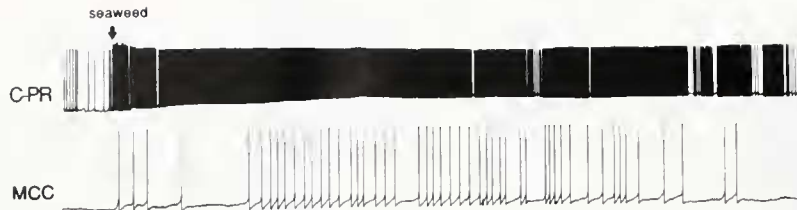
Figure 6. Example of a prolonged excitatory response in C-PR and the MCC to a brief seaweed stimulus. Calibration: 5 s, 20 mV. Data from Teyke *et al.* (1990a).

suggesting that C-PR is probably not directly involved in the directed head turning response, which is very strongly lateralized. Nevertheless, head turning does not occur unless the animal is first aroused, so that C-PR activity may enable head turning. Some of the effects of C-PR are monosynaptic, whereas others are mediated by interneurons. Firing of many of the pedal cells that are affected by the activity of C-PR causes the muscles of the anterior-dorsal region of the neck to contract (Teyke *et al.*, 1990a), which suggests that C-PR may evoke movements that cause the head to be lifted into the feeding posture. Consistent with a role of C-PR in eliciting head-lifting in response to food, we found that seaweed applied to the tentacles evokes strong activity in C-PR (Fig. 6). Furthermore, preliminary studies involving extracellular recordings from the cerebral-pedal connectives, support the idea that C-PR is active just before and during the time that the animal lifts its head into the feeding posture (Teyke *et al.*, 1990c). Thus, the total complex of appetitive feeding responses may consist of two components: a stereotyped postural head-lifting response and a more varied directed turning response.

We have formulated a simple neural model (Teyke *et al.*, 1990b) whose input-output functions are similar to the behavioral results concerning the directed head turning component of appetitive feeding behavior. The model is based on reflex circuits and does not contain command elements. By contrast, the head lifting response may be importantly controlled by a small number of neurons, such as C-PR, that have command-like properties. C-PR, however, affects responses other than head lifting. In fact,
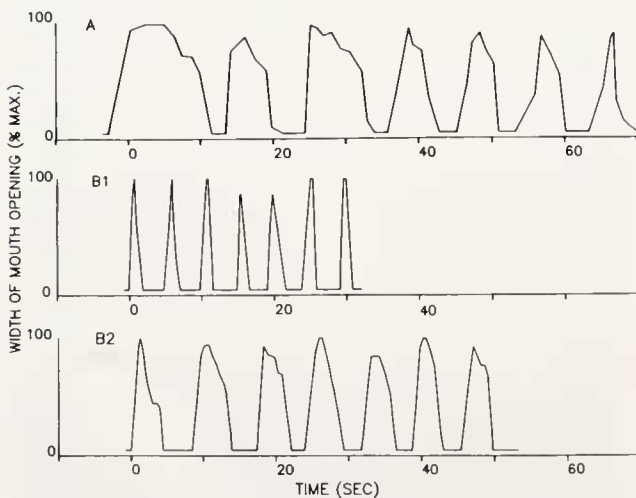

Figure 7. Sequence of mouth openings and closings during seven repetitive biting responses, in two animals that have had bilateral chronic lesions (protease injected) of the MCCs. The sequence is based on a videotaped analysis of biting. Width of the mouth opening is expressed as a percentage of the maximum. A. An example, illustrating "stuck" radula in a MCC lesioned animal, in which the radula stays protracted for an abnormally long duration. B. Responses of a normal animal (B1), and of the same animal (B2) following lesion of the MCCs. Data from Rosen *et al.* (1989a).
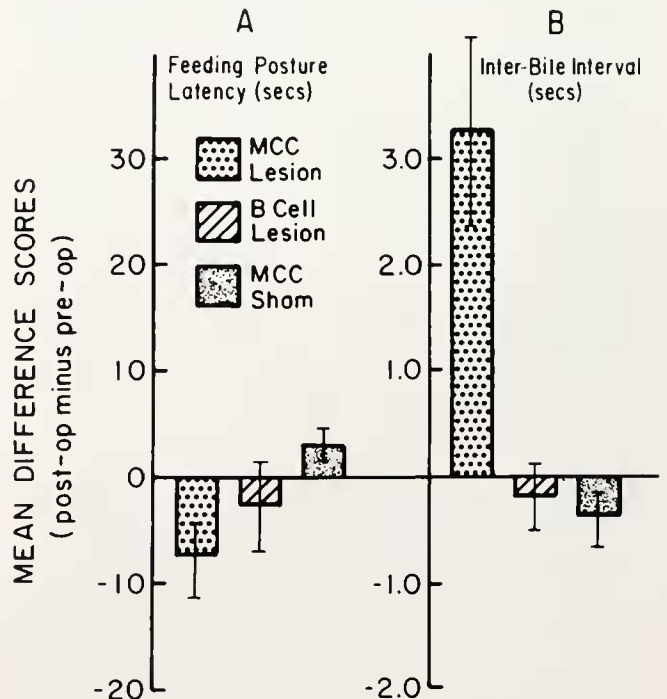

Figure 8. MCC lesion (n = 6), B cell control lesion (n = 7), and dye injection MCC control (n = 6) group mean difference scores (postoperative overall mean, minus preoperative scores, ± SEMs) for latency to assume feeding posture (A) and for interbite interval (B). Bites were elicited by continually stimulating the lips with seaweed, without allowing the animal to obtain the food. Data from Rosen *et al.* (1989a).
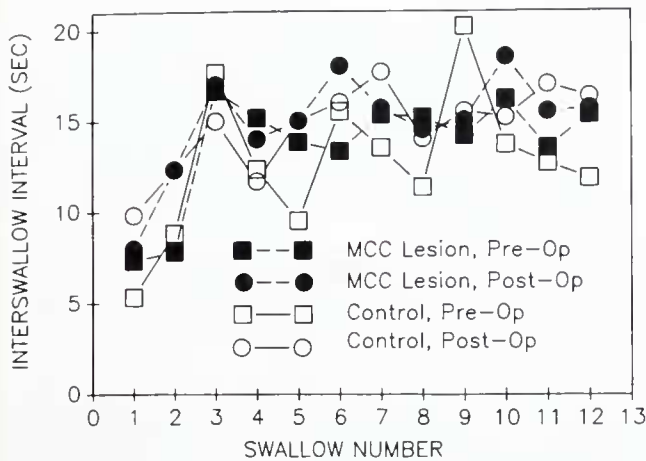
Figure 9. MCC lesion and control groups mean interswallow intervals, measured during ingestion of strips of seaweed. No significant group differences were found. Data from Rosen *et al.* (1989a).

we found that C-PR activity affects neurons involved in three other types of responses: defensive withdrawal reflexes (Fig. 5D), consummatory biting (Fig. 5B), and cardiovascular responses (Fig. 5C). The neurons involved in defensive responses were inhibited by the firing of C-PR, and in semi-intact preparations we showed that the firing of head withdrawal neurons in response to a strong tactile stimulus to the head was reduced when the C-PR neuron was permitted to fire. The rapid depression of withdrawal responses following contact with seaweed may therefore be due either in part, or wholly, to an active inhibition, rather than to low frequency depression, as appears to be the case for habituation of the gill and siphon reflex to tactile stimulation (Castellucci *et al.*, 1970).

Firing of C-PR evokes complex mixtures of excitatory and inhibitory synaptic responses in abdominal ganglion neurons controlling the heart and blood vessels (Fig. 5C). These effects could contribute to aspects of cardiovascular responses that occur during food-induced arousal.

The cerebral ganglion neurons involved in consummatory behaviors generally receive pure excitation when C-PR is fired. These neurons include command-like elements for biting (CBl-2) and the metacerebral cells (MCCs). The MCCs modulate the muscles and neurons that effectuate biting and account, in part, for the build-up of the speed and magnitude of successive bites, which occurs during consummatory arousal (Rosen *et al.*, 1989a). In contrast to the C-PR, the modulatory effects of the MCC are very restricted. It only modulates consummatory responses, and only the bite component. For example, if the MCCs are destroyed, there is no change in the capacity to elicit the feeding posture (Fig. 8) (Rosen *et al.*, 1989a), but there is an increase in the bite latency and inter-bite intervals (Fig. 7, 8B). Inter-swallow intervals are unchanged (Fig. 9).

When C-PR is fired at physiological rates, its excitatory effect on neurons involved in biting responses is never strong enough to drive the neurons at a rate sufficient to evoke biting. C-PR appears to function to increase the excitability of these neurons without directly driving consummatory responses.

By cutting various connectives we could localize the ganglia that contain the interneurons that produce the effects of C-PR on the various non-postural systems. We found that all of these effects are mediated by the activity of the pedal-pleural ganglia. It may be significant that these ganglia mediate the postural responses associated with food arousal. Thus appetitive arousal may involve a primary effect on a postural system, which, in turn, modulates the activity of the numerous other systems that will eventually come into play during feeding. In the vertebrate brain, indeed, neurons thought to be concerned with regulation of consciousness and arousal are concentrated in the brain stem in regions intimately involved with postural regulation (Hobson and Brazier, 1980). Because virtually all behaviors require a particular posture for their execution, the postural neural system may serve a primary role in arousal in highly diverse species.

Some of the effects of C-PR, such as those on the elements of consummatory responses, could enhance these responses. Other effects, such as those on Bn neurons, may suppress responses that are incompatible with feeding behavior. We postulate that C-PR is, in some ways, analogous to command neurons, which evoke behaviors. The C-PR, however, not only evokes a behavior (head lifting), but also evokes a central motive state that aids in insuring that behavior is efficiently expressed. A behavioral action such as feeding is made up of a number of different behavioral acts (*e.g.*, head lifting, biting, swallowing). Thus, a consideration of the ways in which behavioral efficiency is maximized raises two fundamental questions. First, how are multiple responses of the organism coordinated with one another, and second, how are the individual behavioral acts which make up a behavioral action modulated so as to optimize their speed and minimize energy expenditure? Our evidence suggests that one means of coordinating diverse responses directed toward a single goal is to affect diverse neuronal systems through the activity of a relatively few neuronal elements. Data presented elsewhere indicate that maximization of the efficiency of individual responses is accomplished, in part, by the activity of subordinate specialized neurons such as the MCC (Weiss *et al.*, 1978; Rosen *et al.*, 1989a). In addition, individual responses may be regulated by neuromodulators that occur as cotransmitters in motorneurons innervating the muscles that effectuate feeding responses (Lloyd *et al.*, 1985; Cropper *et al.*, 1987a,b, 1988, 1990). The motor neurons are subordinate to the modulatory effects of the MCC, which, in turn, is modulated by C-PR. Thus the

final motor activity appears to be regulated by modulatory neurons of progressively higher order. We are beginning to reduce the elusive concept of motivational state to explanations in terms of the actions of ordinary neural mechanisms, operating in networks of appropriately interconnected neurons.

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